

distally, margined internally by a deep blackish area; sternites uniformly dark brown, the hypopygium more reddish brown.

Hab. New Zealand (North Island).

Holotype, ♂, Ohakune, altitude 2060 feet, December 23, 1921 (*T. R. Harris*).

VIII.—*A Note on the Species as a Gene-complex.*

By GUY C. ROBSON, M.A.

UP to the present no very satisfactory solution of the "species question" has been offered by the geneticist. He has indeed supplied some very just criticisms of the taxonomist's attitude towards the "species," particularly on the question of their origin; but he has nevertheless produced no constructive solution of the problem. The effect of genetic studies in the field of taxonomy has been, in fact, similar to that of the Selection theory. Bateson has pointed out (I, p. 10) the falsification of Darwin's prediction that, when his interpretation was adopted, "the disputes whether or not some fifty species of British brambles are good species or not will cease," only to admit on another page (*l.c.* p. 3), "I cannot assert that we are already in a position to answer this important question" (What is a species?).

In the following note I venture to indicate a method by which at least some precision might be introduced into the discussion. I do not wish to claim originality for these views. They are partly a restatement in a different terminology of those held by other people. I venture to think that such a restatement is necessary at the present time.

We are offered two mutually exclusive views on the nature of species. One is that a species is a purely arbitrary association of individuals agreeing in respect of certain characters, an association justifiable on pragmatical grounds as affording a working basis for the task of classification. The other view is that the species is a biological reality, though no means at present are available for arriving at a satisfactory criterion or of unifying the species-concept as it is applied to the various groups of animals and plants. A number of suggestions have been made as to what such a criterion might

be, ranging from the crude concept of the individual taxonomist's "*flair*" or "eye for a species" to a more serious attempt to synthesize a number of correlated characters after a careful biometrical study of variation in the group.

The latter method seems to offer at least a means of bridging the gap between the taxonomist and the geneticist. We owe to Morgan (5) the concept of the species as a gene-complex. At present this is only a suggestion unelaborated and undeveloped; but it seems to be precisely parallel to the view of certain taxonomists who lay stress on the importance of a number of closely correlated characters.

When animals representative of a "species" are studied intensively by the taxonomist there is revealed a large complex of structural features which exhibit the effects of "specific" differentiation. According to my own experience it is hard to find a system which is not capable of showing the latter. Even glandular structures may be found to exhibit differentiation in two closely related forms, as Kleiner (3) has shown.

It is the composition and fate of the character-complex that has been most neglected in discussions on the nature of species. In practice it has been recognized, but its implications have not been followed up by intensive work on genetic and morphological lines.

We have to ask ourselves, if a species is a complex of constantly associated characters, how does the complex behave in heredity? Are the various characters affected by linkage*? If so, can we ascertain the degree of linkage and thus obtain a standardization of the species? If there is no linkage, what is the nature of the association of characters? Is it purely fortuitous and susceptible of dissociation by crossing? Have we, finally, an advance from unstable character-associations to systems exhibiting linkage in various degrees?

We are certainly not in the position to answer these questions yet; and to suggest lines of research and hint at problems to be solved is perhaps a poor sort of policy. But in the present case any sort of criticism of method is desirable, especially if it affords a *liaison* between two types of research. The writer is constantly impressed in his taxonomic studies of the Mollusca with the instability of the character-complexes conventionally known as "species" and

* The term *linkage* is used here in the general sense of a tendency on the part of certain characters "to keep together rather than to assort freely," Morgan (5, p. 80).

the varying degree to which the characters composing the complex are represented in the individual (*cf.* 6, p. 263). It seems, therefore, that a division of labour is desirable. The anatomist should indicate various types of character-association, and the experimentalist should analyse such cases and assign to them a correct genetic interpretation.

One can imagine that the result of such a study of character-associations might yield one of the results suggested above, viz., every degree of association from the most unstable to the most complete linkage. Would we in such a case be any nearer our goal? The "species" would still be a concept only—a projection of our minds in their search for a *point d'appui* in the perplexing multitude of types of association. We would, however, have arrived at a clearer conception of the way in which the associations originally distinguished as "species" are built up, maintained, or dissociated. We would concentrate less upon the association itself than on the way it is represented in the individual.

In practice we find it increasingly difficult, as animals are subjected to a more intensive study, to make our rigid concepts fit the facts of Nature. Not only species but genera and families appear to be mere abstractions which form a sort of "Bed of Procrustes" in which the affinities of animals are often painfully distorted in order to fit the inelastic framework. On the other hand, it is obvious that we cannot relapse into a passive acceptance of an animal kingdom wholly anarchic in the relationship of its units. The observations of competent field-naturalists and taxonomists show us that some associations at least are permanent. The fault of taxonomy in the past seems to have been not that its units are unreal, but that it has extended them unwarrantably. A well-known case may make the above generalizations clearer.

The two species of snail, *Tachea hortensis* and *T. nemoralis*, are widely distributed in West and Central Europe. They have been the objects for many years of a solicitous examination usually made in order to answer the questions: "Are they two species, and, if so, what is the real difference?"

These studies were originally conchological, but the number of structures examined has been increased and breeding experiments have been conducted with the animals. One of the chief results for our purpose is that places are known where the pure *hortensis* shell-form is obtained either with or without the pure *nemoralis* shell-form, and *vice versâ*. On

the other hand, we find localities where "intermediates" * occur. Examination of these various types have been principally conchological, and it has been concluded that all the shell-characters are completely "transgressive" *. A more limited examination of the genitalia indicates that these organs are also transgressive. An exception has been invariably made in the case of the *dart*. It is usually stated that the latter is the only criterion of distinctness. There now appears to be doubt even on this subject.

We have also cases where the *hortensis* and *nemoralis* complexes are modified so as to render distinction impossible. Information is less plentiful about the relation of these "species" to the other *Tacheas*. But it is possible that they have the same indeterminate relationship with *T. austriaca*.

Before completing our review of this case we must briefly consider the *dart* as a criterion of distinctness. As we have pointed out above, there is some doubt whether it is not also transgressive. A new difficulty is, however, created by the discovery by Lang (4), Kleiner (3), and Boettger (2) that the *dart* itself behaves not as a unit but as a complex. Eight characters can easily be distinguished in it, and, according to the results of Lang and Kleiner, the darts of the F_1 hybrids are a "mosaic" of *hortensis*, *nemoralis*, and intermediate characters! Furthermore, all the hybrids did not exhibit the same combination.

We thus see that in this case the search for an absolute criterion breaks down. Our gene-complex appears to be a constant association only in certain cases. At one time we find an association of extreme *hortensis* or *nemoralis* characters; and we might be justified in recognizing such compact groups of characters as "species." But in other cases we find groupings which we can only assign to one or the other of the two extreme types by an obvious *petitio principii*—an appeal to the *dart*. In assigning such forms to one or another of the two "species" we are certainly not indicating their real relationship, which is one that cannot be expressed by crudely contrasted names. What we require is some system that expresses the different modes of character-combination.

It is very much to be regretted that up to the present no satisfactory F_2 results have been obtained from crossing the extreme forms. If an increased knowledge of the necessary vital conditions is successful in producing a third generation,

* The terms "intermediate" and "transgressive" have been used in this note without qualification. In the circumstances, a discussion of the precise meaning of such types of variation seems to be unnecessary.

we shall be in a better position to discuss the behaviour of the various characters and to decide whether linkage is present.

In the meantime, the discussion whether there are two "species" or one in this case is probably placed in its true perspective. In the first place, we see that the species-concept is too rigid to apply to such a variety of indeterminate character-associations. Even if we single out the extreme associations and oppose them under different names, we are merely confusing the issue by stressing the extremes and ignoring the more indeterminate combinations. In the second place, we do not know whether these particular extreme associations are analogous to others in which linkage occurs, though we might be tempted to predict from the combinations found in the field that they are not.

SUMMARY.

(1) There is urgent necessity for the investigation of the "species" as a character-complex. The subject should be studied both from its genetic and its morphological aspect.

(2) The character-complex is a fact of common knowledge. Viewed at the morphological level it varies extensively in its components, exhibiting a correlated system of non-transgressive characters or showing a large variety of combinations which include transgressive characters.

(3) The future method of investigation should be an attempt to discover whether linkage occurs in such associations, and, if so, to what extent.

(4) Improved morphological and genetic investigation of the degree to which the complex is represented in *individuals* is likely to show that any attempt to distinguish rigid categories among associations of such variable constitution is a very imperfect representation of the relations between organisms. The "species" concept, as far as we can see without further investigation along these lines, appears to be applicable to only a certain type of combination.

WORKS QUOTED.

- (1) BATESON. 'Problems of Genetics.' 1913.
 - (2) BOETTGER. Zool. Jahrb. xlv. Syst. 1921.
 - (3) KLEINER. "Untersuchungen am Genitalapparat von *H. nemoralis* und *hortensis*." Inaugural Dissertation. Zurich.
 - (4) LANG. 'Ueber die Bastarde von *H. hortensis* und *H. nemoralis*.' Jena, 1908.
 - (5) MORGAN. "The Physical Basis of Heredity." (Monographs on Experimental Biology.) 1911.
- ROBSON. Proc. Zool. Soc. 1921.